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Macroevolution and shifts in the feeding biology of the New World scarab beetle tribe Phanaeini (Coleoptera: Scarabaeidae: Scarabaeinae)

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The New World scarab beetle tribe Phanaeini contains coprophagous, necrophagous, mycetophagous and suspected myrmecophilous species. We analyse the largest tribal molecular dataset assembled, incorporating, for the first time, the enigmatic monobasic genus *Megatharsis*, the *thalassinus* group of the subgenus *Coprophanaeus* (*Metallophanaeus*), and the subgenus *Dendropaemon* (*Eurypodea*) (formerly *Tetramereia*), unveiling their macroevolutionary and biogeographical history in light of Cenozoic abiotic changes and inferring shifts in feeding biology through time. We recover the contentious genus *Gromphas* outside an otherwise monophyletic Phanaeini. We infer *Megatharsis* in a clade containing the apparent myrmecophilous genus *Dendropaemon*, within the *Coprophanaeus* clade, and demonstrate that the subgenus *Coprophanaeus* (*Metallophanaeus*) is polyphyletic, whilst species groups within the subgenus *Coprophanaeus* (*Coprophanaeus*) are monophyletic. Our divergence time analyses and ancestral range estimation indicate an eastern South American origin for Phanaeini in the early Eocene, with subsequent colonization of Central America and the Nearctic during the Oligocene, long before a Panamanian land bridge. A shift to necrophagy in *Coprophanaeus* is possibly linked to increasing Neotropical small vertebrate diversity since the Eocene and, astonishingly, myrmecophily evolved from necrophagy 35 Mya. These drastic shifts in lifestyle are not concordant with variations in diversification rates and appear unlinked to Quaternary extinction of large mammals.

ADDITIONAL KEYWORDS: *Coprophanaeus* – *Dendropaemon* – diet evolution – dung beetles – Eocene – *Megatharsis* – *Metallophanaeus* – necrophagy – Panamanian land bridge – *Tetramereia*.

> Le fouilleur d'ordure ferait honneur aux écrins du joaillier
> – Jean-Henri Fabre, 1899, *Souvenirs Entomologiques*

INTRODUCTION

Dung beetles of the subfamily Scarabaeinae are a diverse group of ~6000 species, currently divided into 12 tribes, although disagreements exist regarding this higher classification scheme (Tarasov & Dimitrov, 2016). These beetles encompass a great variety in morphology and occupy most of the major ecosystems in every zoogeographical region except Antarctica (Scholtz *et al.*, 2009). Contrary to what their vulgar name might suggest, scarabaeine 'dung beetles' as a whole are not restricted to feeding on vertebrate (or invertebrate) dung. In fact, the niches that they fill comprise diverse and occasionally highly specialized feeding biologies, including, but not limited to necrophagy (vertebrate and invertebrate), mycetophagy, frugivory, invertebrate predation, phoresy and myrmecophily, in addition to a variety of food-relocation behaviours (e.g. the generalized 'rolling', 'tunnelling' and 'dwelling' behaviours; Halffter & Matthews, 1966; Hanski & Cambefort, 1991; Scholtz *et al.*, 2009; Simmons *et al.*, 2011). Dung beetles have proved to be a reliable 'proxy' group for understanding wider biodiversity patterns, primarily owing to the dependance of most species upon vertebrate dung or carrion. They have consequently been adopted as a cost-effective bioindicator taxon often incorporated into biodiversity assessment (Halffter & Favila, 1993; Spector, 2006; Gardner *et al.*, 2008; Gillett *et al.*, 2016).

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However, a combination of co-declining mammal and dung beetle communities (Schweiger & Svenning, 2018; Bogoni *et al.*, 2019), the adverse effects on dung beetle populations caused, in part, by human-induced habitat and climate change (e.g. Horgan, 2005; Larsen, 2011) and the negative non-target consequences of anti-parasitic preventative medicine administered to livestock (e.g. Verdú *et al.*, 2015, 2018) is evidence that these beneficial insects are progressively threatened and worthy of concern and study. Being a common component of most New World dung beetle communities, and therefore contributing to the corresponding associated ecosystem services provided by such communities, including nutrient cycling and secondary seed dispersal (Nichols *et al.*, 2008), the tribe Phanaeini is assuredly an important group for study and has been investigated as an integral component of many studies into dung beetle communities across several of the regions in which they occur (e.g. Gillett *et al.*, 2010; Da Silva *et al.*, 2013; Daniel *et al.*, 2014; Medina & Lopes, 2014; Salomão & Iannuzi, 2015).

From a purely taxonomic standpoint, the New World-exclusive tribe Phanaeini is counted among the best-known groups of scarab beetles. At present, it is understood to consist of 189 extant species within two subtribes and 11 genera, the majority of which have been the subject of recent taxonomic review (Arnaud, 2002; Edmonds, 1994, 2000; Edmonds & Zídek, 2004, 2010, 2012; Cupello & Vaz-de-Mello, 2013, 2014a, 2016; Génier & Arnaud, 2016; Valois *et al.*, 2020). The larger subtribe Phanaeina comprises the genera *Bolbites* Harold, 1868 (one sp.), *Coprophanaeus* d'Olsoufieff, 1924 (44 spp. in three subgenera), *Dendropaemon* Perty, 1830 (41 spp. in 12 subgenera), *Diabroctis* Gistel, 1857 (five spp.), *Homalotarsus* Janssens, 1932 (one sp.), *Megatharsis* Waterhouse, 1891 (one sp.), *Oxysternon* Laporte, 1840 (11 spp.), *Phanaeus* MacLeay, 1819 (63 spp. in two subgenera) and *Sulcophanaeus* d'Olsoufieff, 1924 (14 spp.), whilst the smaller subtribe Gromphadina consists of only *Gromphas* Brullé, 1837 (six spp.) and *Oruscatus* Bates, 1870 (two spp.) (Cupello & Vaz-de-Mello, 2016) (Figs 1–3). New species continue to be discovered, with no fewer than eight new species of *Phanaeus* having been described within the last 3 years alone (Moctezuma *et al.*, 2017, 2019, 2020; Moctezuma & Halffter, 2017; Arnaud, 2018; Kohlmann *et al.*, 2018).

Although most species of Phanaeini are coprophagous, the genus *Coprophanaeus* is widely reported as necrophagous, whilst at least one species of *Phanaeus* (*Phanaeus halffterorum* Edmonds, 1979) is recorded as being mycetophagous, and others are suspected to be inquilines in the burrows of small mammals (Edmonds, 1972, 1994; Philips *et al.*, 2004; Price & May, 2009; Scholtz *et al.*, 2009; Edmonds & Zidek, 2010; Simmons & Ridsdill-Smith, 2011). However, the most extraordinary biology that is associated with the tribe is myrmecophily. Several species of the morphologically specialized *Dendropaemon* have been associated with leaf-cutter ants of the genus *Atta* Fabricius, 1805 (Formicidae), and a similar association is suspected for the enigmatic and very rare monobasic genera *Homalotarsus* and *Megatharsis* (Vaz-de-Mello *et al.*, 1998; Philips *et al.*, 2004; Larsen *et al.*, 2006; Gillett *et al.*, 2009; Vaz-de-Mello & Génier, 2009). All three of the suspected myrmecophilous genera share certain morphological traits, including highly modified meso- and meta-tarsi (with the number of tarsal segments in *Dendropaemon* reduced to as few as two), attenuation or loss of sexual dimorphism, and a generalized diminution in body size (Figs 1G-I, 2B, 3). Génier & Arnaud (2016) discuss a number of morphological characters that suggest a derived feeding behaviour and possible association with an inquilinous lifestyle in *Dendropaemon*.

The combined distribution of the Phanaeini covers a large portion of the Americas, stretching from northern Argentina (~39°S) northwards to the central USA (~44°N). The majority of species occur in the Neotropical region, where all 11 genera are represented, although several species occur in the Nearctic, and there is extensive diversity in the complicated Mexican transition zone between the two biogeographical regions. At present, the tribe is notably absent from most of the western regions of the central Andes, which correspond to true desert or altiplano areas, and the adjacent arid coastal plain. It is present, however, in the dry coastal areas of southern Ecuador and the far north of Peru. It is also absent from areas west of the Rocky Mountains in North America and from all of the Greater and Lesser Antilles, except Jamaica (Edmonds, 1972, 1994; Edmonds & Zidek, 2010).

Philips *et al.* (2004) hypothesized that the Phanaeini originated in South America subsequent to its separation from Africa during the late Mesozoic. They contemplated that the tribe later colonized Central and North America after the formation of the Panamanian land bridge during the late Pliocene. Scholtz *et al.* (2009) speculated that the (generally large) Phanaeini evolved in response to increased availability of dung, resulting from the rise of the Neotropical mammalian megafauna during the Miocene. Furthermore, it has been widely hypothesized that the subsequent extinction of the majority (~75% of species) of these large mammals during the Pleistocene might have prompted dietary switches to alternative food sources, including carrion and fungi, and to myrmecophily (Halffter & Matthews, 1966; Halffter & Halffter, 2009; Scholtz *et al.*, 2009). Based on a combined morphological (67 characters) and molecular (1155 bp of mitochondrial cytochrome *c* oxidase and ribosomal 28S rRNA) phylogenetic analysis of the genus *Phanaeus*, in combination with dispersal

Figure 1. Diversity of major lineages of the New World scarab beetle tribe Phanaeini. A–L, representative species of the New World scarab dung beetle tribe Phanaeini, demonstrating generic and subgeneric morphological and colour diversity, sexual dimorphism and size variation. The male is on the left side of each photograph depicting a pair. A, *Coprophanaeus* (*Megaphanaeus*) *lancifer* (Linnaeus, 1767) pair in Suriname. B, *Coprophanaeus* (*Coprophanaeus*) *acrisius* (MacLeay, 1819) pair in Brazil. C, *Oxysternon* (*Mioxysternon*) *festivum* (Linnaeus, 1758) pair in Suriname. D, *Oxysternon* (*Mioxysternon*) *spiniferum* Castelnau, 1840 pair in French Guiana. E, *Phanaeus* (*Phanaeus*) *vindex* MacLeay, 1819 pair in

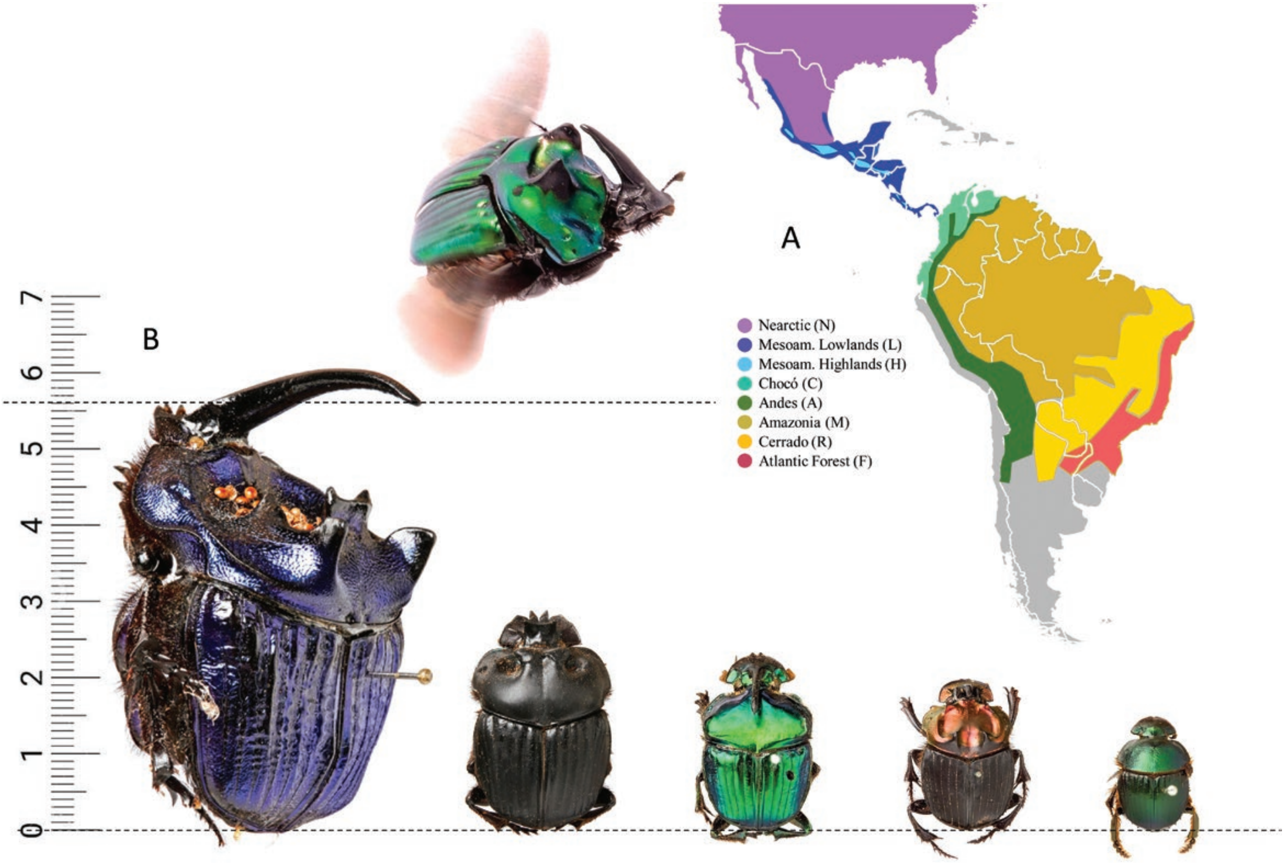

Figure 2. Map of New World biogeographical regions, and size variation in Phanaeini. A, map of the New World, depicting the simplified system of biogeographical regions used in the ancestral range estimation analysis. Inset shows in-flight male *Oxysternon* (*Oxysternon*) *lautum* (MacLeay, 1819) in Peru; photograph by Martin Taylor, Eve Corey, and Conrad P. D. T. Gillett. B, variation in size within the tribe Phanaeini, illustrated by five species demonstrating the five size categories implemented in the ancestral size analysis, from left to right (scale in centimetres and millimetres): very large, *Coprophanaeus* (*Megaphanaeus*) *lancifer*; large, *Coprophanaeus* (*Coprophanaeus*) *dardanus* (MacLeay, 1819); medium, *Phanaeus* (*Notiophanaeus*) *kirbyi* Vigors, 1825; small, *Sulcophanaeus noctis* (Bates, 1887); and very small, *Megatharsis buckleyi*. Specimens are shown to scale, demonstrating maximum recorded lengths for each species. Photographs by Harry Taylor.

vicariance computational reconstructions, Price (2009) concluded that ancestral species of this diverse genus arose in the Andean mountains and, subsequently, dispersed into the Amazon basin. The genus afterwards colonized and further diversified in what is now southern Brazil and the Guiana Shield. Nonetheless, these recent hypotheses remain to be tested based on estimates of absolute divergence times and quantitative ancestral range estimations. An Eocene to Oligocene crown age for Phanaeini was inferred by Scholtz *et al.* (2009) and Davis *et al.* (2017) based upon different age calibrations of the proportional distance data presented in the dispersal vicariance analysis (DIVA) dendrogram of Monaghan *et al.* (2007). However, in a recent study, Gunter *et al.* (2016) recovered a crown age estimate for Phanaeini (represented by the genera *Coprophanaeus*, *Dendropaemon*, *Oxysternon* and *Phanaeus*) in the Eocene, between 32 and 51 Mya, depending on the calibration strategy. Therefore, a more in-depth investigation of divergence times across most genera

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the USA. F, *Phanaeus* (*Notiophanaeus*) *bispinus* Bates, 1868 pair in Suriname. G, *Megatharsis buckleyi* Waterhouse, 1891 in Ecuador. H, *Gromphas aeruginosa* (Perty, 1830) male in Peru. I, habitus of *Megatharsis buckleyi* Waterhouse, 1891, from Ecuador. J, habitus of male *Diabroctis pseudomimas* Valois, Vaz-de-Mello & Silva, 2020, from Brazil. K, habitus of male *Coprophanaeus* (*Metallophanaeus*) *pertyi* from Brazil. L, habitus of male *Coprophanaeus* (*Megaphanaeus*) *ensifer* (Germar, 1821) from Brazil. Photographs A–H and acrylic paintings I–L are by Conrad P. D. T. Gillett. All images © the photographer.

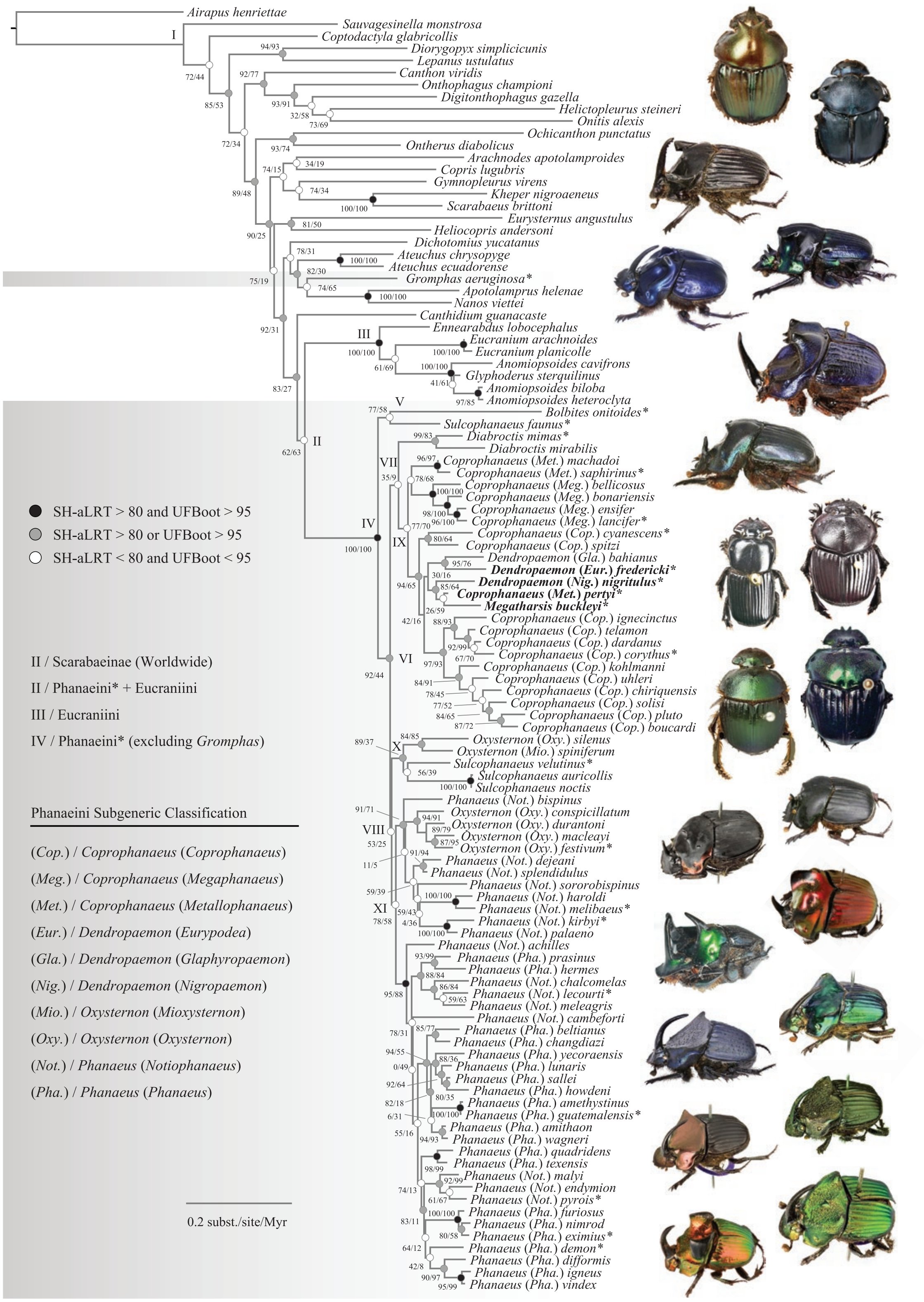

Figure 3. Maximum likelihood phylogenetic reconstruction of Scarabaeinae, with a focus on Phanaeini. Best-scoring maximum likelihood tree selected among 300 independent tree searches performed in IQ-TREE with a heuristic search for optimal dataset partitioning and models of nucleotide substitution based on a concatenated dataset of five gene fragments

is needed to understand the evolutionary history of Phanaeini in the Neotropical and Nearctic regions.

Philips *et al.* (2004) were the first to demonstrate explicitly that the sister group to Phanaeini is the Neotropical tribe Eucraniini (endemic to Argentina) and not, as had been previously hypothesized, the Old World tribe Onitini (Zunino, 1985). This sister relationship between Phanaeini and Eucraniini has been corroborated by several subsequent subfamily-level molecular phylogenies (Ocampo & Hawks, 2006; Monaghan *et al.*, 2007; Gunter *et al.*, 2016; Tarasov & Dimitrov, 2016). Notwithstanding the relatively stable intrageneric alpha taxonomy of Phanaeini, which has, for a long time, been based overwhelmingly upon the study of morphological characters, the phylogenetic basis underpinning the infrageneric classification has been far less extensively explored and questioned. Moreover, to date, no comprehensive study focusing on the entire tribe and based on molecular data has been attempted. Only a single (morphological) study has hitherto analysed phylogenetic data gleaned from the bulk of the constituent genera of Phanaeini (Philips *et al.*, 2004). That study, which incorporated all Phanaeini genera except the monobasic *Homalotarsus* (known from only two specimens), demonstrated the monophyly of the tribe and was characterized by a suite of synapomorphies (Philips *et al.*, 2004). Before that study, considerable uncertainty existed concerning the inclusion of the genera *Bolbites*, *Gromphas* and *Oruscatus* within Phanaeini (e.g. Edmonds, 1972). Although Edmonds (1972) omitted the three aforementioned genera from the 'phanaeine' assemblage in his comprehensive review of the morphology of Phanaeini, he did not attempt to transfer them elsewhere, owing to uncertainty in their alternative placement within the Scarabaeinae. Conversely, however, Philips *et al.* (2004) concluded that the monophyly of Phanaeini was 'unaffected by the inclusion' of those three genera.

One evolutionary hypothesis presented by Philips *et al.* (2004) inferred the purported myrmecophilous genera (*Dendropaemon* + *Homalotarsus* + *Megatharsis*) as derived Phanaeini belonging to a clade sister to the predominantly necrophagous *Coprophanaeus*, with this combined necrophagous/myrmecophilous clade being sister to a clade containing the overwhelmingly coprophagous *Phanaeus*, *Oxysternon* and *Sulcophanaeus* (in part) followed, in turn, by *Diabroctis*, the remaining *Sulcophanaeus* and *Bolbites* as progressively basal sister taxa, with *Gromphas* and *Oruscatus* together forming a clade sister to all other Phanaeini.

Intratribal phylogenetic studies have hitherto been attempted for *Phanaeus* (Price, 2007, 2009), *Oxysternon* (Cuadrado-Ríos *et al.*, 2013), *Gromphas* (Cupello & Vaz-de-Mello, 2016), *Dendropaemon* (Génier & Arnaud, 2016) and *Coprophanaeus* [with a focus on the subgenus *Coprophanaeus* (*Megaphanaeus*); Maldaner *et al.*, 2020]. The diverse genus *Phanaeus* is divided into two subgenera, with *Phanaeus* (*Notiophanaeus*) Edmonds, 1994, a principally South American subgenus, being essentially distinguishable from the nominate subgenus by the arguably subjective extent of surface sculpturing. A morphological phylogeny of *Phanaeus* (Price, 2007) concluded that *Phanaeus* is monophyletic with the inclusion of *Oxysternon* nested within it. This scenario was not supported by a subsequent combined three-gene molecular and morphological reconstruction of the same genus (Price, 2009), in which the monophyly of *Phanaeus* could not be supported, even with the inclusion of *Oxysternon*. Several broader analyses of the evolution of Scarabaeinae, incorporating solely molecular data, are consistent with a sister relationship between *Phanaeus* and *Oxysternon*, albeit in all cases based upon very limited taxon sampling in these two genera (Monaghan *et al.*, 2007; Gunter *et al.*, 2016; Tarasov & Dimitrov, 2016). A limited phylogenetic analysis of four species of *Oxysternon* (Cuadrado-Ríos *et al.*, 2013) contained only a single *Phanaeus* species as an outgroup and therefore could not offer insights into the relationship between these genera.

In their revision of *Dendropaemon*, Génier & Arnaud (2016) undertook a morphological phylogenetic analysis of all its constituent species [including those formerly in the genus *Tetramereia* Klages, 1907, placed by the authors into the subgenus *Dendropaemon* (*Eurypodea*) Klages, 1906] together with the other purported myrmecophilous genera, *Homalotarsus* and *Megatharsis*. They recovered a monophyletic *Dendropaemon*, with *Homalotarsus* and *Megatharsis* basal to it, thereby together forming a 'myrmecophilous' (our emphasis) clade (Génier & Arnaud, 2016), which was, likewise, inferred in

(16S, 18S, 28S, *CO1* and *CYTB*). Nodal support values calculated in IQ-TREE are reported in the topology (SH-aLRT tests/UFBoot). An additional colour coding indicates nodal robustness as detailed in the inset key. Details of the subgeneric classification within Phanaeini are given along with dorsal and lateral photographs of representative Phanaeini species. Name labels of species never included in a molecular phylogenetic framework before are in bold. Species for which a representative is illustrated are indicated by an asterisk after the taxon label (ordering of photographs is from top to bottom, mirroring the order of taxa with asterisks along the tree). Photographs are by Harry Taylor, François Génier, Udo Schmidt (licensed under Creative Commons Attribution-ShareAlike 2.0) and Conrad P. D. T. Gillett.

most of the morphological analyses of Philips *et al.* (2004). A phylogenetic reconstruction focusing on the subgenus *Coprophanaeus* (*Megaphanaeus*), based upon analysis of four molecular markers, concluded that this taxon, consisting of the largest species of Phanaeini, is monophyletic with the inclusion of *Coprophanaeus bellicosus* (Olivier, 1789), an Atlantic Forest species previously of contentious placement within the subgenus (Maldaner *et al.*, 2020). Having also incorporated, for the first time, in that analysis sequence data from the subgenus *Coprophanaeus* (*Metallophanaeus*) d'Olsoufieff, 1924, the authors were able to demonstrate a close relationship between *Coprophanaeus* (*Metallophanaeus*) and *Coprophanaeus* (*Megaphanaeus*), which were recovered together in a clade sister to the nominate subgenus *Coprophanaeus* (*Coprophanaeus*). However, because *Coprophanaeus* (*Metallophanaeus*) is itself composed of two rather distinct species groups [the *Coprophanaeus* (*Metallophanaeus*) *saphirinus* (Sturm, 1826) and the *Coprophanaeus* (*Metallophanaeus*) *thalassinus* (Perty, 1830) species groups] but only two species belonging to one species group were analysed by Maldaner *et al.*, 2020), the precise relationship among the subgenera of *Coprophanaeus* remains uncertain. A second molecular analysis of *Coprophanaeus* (*Megaphanaeus*), which focused on exploring intraspecific variation within *Coprophanaeus ensifer* (Germar, 1821), revealed that despite considerable morphological and colour variation in that species, the molecular evidence did not support recognition of any cryptic species (Maldaner *et al.*, 2019).

In the present study, we aim to infer the first dated molecular phylogenetic reconstruction focused on the tribe Phanaeini, based upon analysis of the largest dataset compiled for this tribe to date, and containing all genera of Phanaeini but two (*Homalotarsus* and *Oruscatus*; see Material and Methods). Our dataset combines newly sequenced DNA data (capitalizing on fortuitous sampling of rare and enigmatic taxa) with existing publicly available sequence data from online repositories. Renewed analysis of such enriched 'legacy' data, often with a concomitant expansion in taxon sampling, has been used successfully to glean compelling insights into the evolution of a variety of taxa (e.g. Jønsson *et al.*, 2016; Zheng & Wiens, 2016; Amador *et al.*, 2018; Shin *et al.*, 2018; Toussaint & Gillett, 2018; Tu *et al.*, 2018; Gough *et al.*, 2019; Sun *et al.*, 2019). We specifically incorporate the first sequence data available from the enigmatic monobasic genus *Megatharsis* and the subgenus *Dendropaemon* (*Eurypodea*) (Figs 1G, I, 2B, 3) in order to infer their relationship within the tribe and test this against morphological hypotheses suggesting a close affinity of those taxa to the other myrmecophilous genera (Philips *et al.*, 2004). Likewise, we also incorporate, for the first time, sequence data from the *C.* (*Metallophanaeus*) *thalassinus* species group in order to test the hypothesis of Edmonds & Zidek (2010) that the subgenus is paraphyletic. We apply our dated phylogeny to infer biogeographical scenarios of Phanaeini divergence and discuss the possible evolution of a variety of atypical feeding biologies exhibited by the group.

MATERIAL AND METHODS

Taxon sampling and dataset construction

We used Sanger sequencing to generate new sequence data for key Phanaeini taxa missing from public sequence repositories. Specifically, we sequenced molecular data for the species *Bolbites onitoides* Harold, 1868, *Coprophanaeus* (*Coprophanaeus*) *cyanescens* (d'Olsoufieff, 1924) and, for the first time, *Coprophanaeus* (*Metallophanaeus*) *pertyi* (d'Olsoufieff, 1924) [belonging to the *C.* (*Metallophanaeus*) *thalassinus* species group], *Megatharsis buckleyi* Waterhouse, 1891, *Dendropaemon* (*Eurypodea*) *fredericki* (Klages, 1906) [formerly widely known as *Tetramereia convexa* (Harold, 1869)] and *Dendropaemon* (*Nigropaemon*) *nigritulus* Génier & Arnaud, 2016 (Figs 1G, I, K, 3B). This also represents the first time that the last four species and their respective genera or subgenera (or species group, in the case of *C. pertyi*) have been sequenced. All newly generated sequence data are deposited in GenBank (accession numbers MT313695-MT313709).

To infer a comprehensive molecular phylogeny of the tribe Phanaeini, we also sampled all published DNA sequence data from GenBank (Benson *et al.*, 2018) and BOLD (Ratnasingham & Hebert, 2007). In total, we sampled 74 Phanaeini species, including representatives of the genera *Coprophanaeus* [including the three recognized subgenera: *Coprophanaeus* (*Coprophanaeus*), *Coprophanaeus* (*Megaphanaeus*) and *Coprophanaeus* (*Metallophanaeus*)], *Dendropaemon* [three of the 12 recognized subgenera: *Dendropaemon* (*Nigropaemon*) Génier & Arnaud, 2016, *Dendropaemon* (*Glaphyropaemon*) Génier & Arnaud, 2016 and *Dendropaemon* (*Eurypodea*)], *Diabroctis*, *Gromphas*, *Megatharsis*, *Oxysternon* [including the two recognized subgenera: *Oxysternon* (*Oxysternon*) and *Oxysternon* (*Mioxysternon*) Edmonds, 1972], *Phanaeus* [including the two recognized subgenera: *Phanaeus* (*Phanaeus*) and *Phanaeus* (*Notiophanaeus*)] and *Sulcophanaeus*, corresponding to ~40% of the described species-level diversity of the tribe. We included a comprehensive number of outgroups from the subfamily Scarabaeinae to test the monophyly of Phanaeini inferred in earlier molecular studies (Monaghan *et al.*, 2007; Gunter *et al.*, 2016; Tarasov & Dimitrov, 2016). We are aware that the inclusion of so many outgroups with a reduced molecular dataset is likely to result in poorly resolved higher-level phylogenetic relationships, but the main rationale for inclusion of these external lineages is to test the monophyly of Phanaeini and, if not recovered, the placement of lineages that would branch outside of the main clade. The tree was rooted with *Airapus henriettae* Stebnicka & Howden, 1996 (Scarabaeidae, Aphodiinae) following Gunter *et al.* (2016).

All data were imported into GENEIOUS R11 (Biomatters, USA) for cleaning and alignment. We quality checked every sequence and inferred gene trees to eliminate potential contamination and misidentifications. We gathered molecular sequence data for the following five gene fragments: mitochondrial ribosomal 16S (463 bp), mitochondrial cytochrome *c* oxidase subunit 1 (*CO1*, 1455 bp), mitochondrial cytochrome *b* (*CYTB*, 330 bp), nuclear ribosomal 18S (18S, 1910 bp) and nuclear ribosomal 28S (28S, 1534 bp). Although a single sequence of 18S exists in GenBank for the genus *Oruscatus*, preliminary gene tree inference revealed alignment problems, and the sequence was later discarded from the dataset. For the newly sequenced taxa outlined above, PCR primers, amplification and sequencing protocols followed Shull *et al.* (2001) and Gillett *et al.* (2014). The ribosomal gene fragments were aligned using MAFFT v.7.450 (Katoh & Standley, 2013) with the G-INS-i algorithm (scoring matrix: 200PAM/$k = 2$) and a gap open penalty of 1.53. The protein-coding gene fragments were aligned with MUSCLE v.3.8.425 (Edgar, 2004) with default settings. After quality checking, all curated gene fragment alignments were concatenated in GENEIOUS and exported for further phylogenetic inferences. The resulting molecular dataset, comprising 5692 bp and 106 taxa, is available in the Supporting Information (Appendix S1).

Phylogenetic inference

We estimated the best partitioning scheme and corresponding models of nucleotide substitution for the concatenated dataset with ModelFinder (Kalyaanamoorthy *et al.*, 2017) as implemented in IQ-TREE v.1.6.9 (Nguyen *et al.*, 2015; Supporting Information, Appendix S2). We partitioned the dataset a priori by codon positions for the protein-coding gene fragments and by locus for the ribosomal gene fragments, for a total of nine initial partitions. In order to minimize the risk of a local optimum, we conducted 300 independent maximum likelihood (ML) tree searches in IQ-TREE. We assessed nodal support with two metrics: the ultrafast bootstrap (UFBoot) (Minh *et al.*, 2013; Hoang *et al.*, 2018) and the SH-aLRT tests (Guindon *et al.*, 2010), generating 1000 replicates for each. To reduce the risk of overestimating branch support with UFBoot owing to severe model violations, we used a hill-climbing nearest-neighbour interchange (NNI) topology search strategy to optimize each bootstrap tree.

Divergence time estimation

We estimated divergence times among Phanaeini beetles in a Bayesian framework with BEAST v.1.10.4 (Suchard *et al.*, 2018). Given that the focus of this study was the evolution of the tribe Phanaeini and not that of Scarabaeinae as a whole, we restricted the dataset to only Phanaeini and their sister tribe Eucraniini, and included *Ateuchus chrysopyge* (Bates, 1887) as an outgroup based on the IQ-TREE results (see Results).

The best partitioning scheme and models of substitution were determined in PartitionFinder2 (Lanfear *et al.*, 2017) using the *greedy* algorithm and the Bayesian information criterion across all models included in BEAST. We implemented clock partitioning by conducting analyses with: (1) a single clock for all partitions; (2) two clocks, one for the mitochondrial gene fragments (16S, *CO1* and *CYTB*) and one for the nuclear gene fragments (18S and 28S); and (3) one clock for each partition (six in total, according to the PartitionFinder results). We assigned a Bayesian lognormal relaxed clock model to the different clock partitions. We also tested different tree models by using a Yule (pure birth) speciation or a birth–death model in different analyses. Analyses consisted of 50 million generations, with a parameter and tree sampling every 5000 generations. We estimated marginal likelihood estimates (MLEs) for each analysis using path-sampling and stepping-stone sampling (Baele *et al.*, 2013), with 1000 path steps, and chains running for one million generations with a log-likelihood (LnL) sampling every 1000 cycles. The maximum clade credibility (MCC) trees of each analysis with median divergence age estimates were generated in TreeAnnotator v.1.10.4 (Suchard *et al.*, 2018) after removing the first 12.5 million generations as burn-in.

Given that the fossil record of Phanaeini is unknown except for an undated specimen retrieved from an ichnofossil (Edmonds, 1972; Zunino, 2013), we relied upon the dating scheme developed by Gunter *et al.* (2016) to infer absolute ages of divergence in BEAST. In that study, the authors inferred a molecular phylogeny of Scarabaeinae using three gene fragments (16S, 28S and *CO1*). They subsequently estimated divergence times among Scarabaeinae using different calibration strategies that relied upon described fossils (see also Ahrens *et al.*, 2014). To estimate divergence times within Phanaeini, we used secondary calibrations derived from Gunter *et al.* (2016) to constrain three nodes with intervals encompassing the credibility intervals of their most realistic analyses (CSiii, CS2 and CS3; N. Gunter, pers. comm.). As a result, we constrained the root of the tree (*Ateuchus chrysopyge* + Eucraniini + Phanaeini) with a uniform prior having a maximum hard bound of 96.7 Mya and a minimum hard bound of 67.3 Mya, corresponding respectively to the highest and lowest values of 95% credibility intervals across the three analyses (CSiii, CS2 and CS3 from the study by Gunter *et al.* (2016). In a similar way, we constrained the crown of Eucraniini + Phanaeini (minimum, 58.2 Mya; maximum, 90.0 Mya) and the crown of Eucraniini (minimum, 36.3 Mya; maximum, 68.4 Mya) with uniform priors. These three nodes were also recovered by Tarasov & Dimitrov (2016), in the most comprehensive phylogenetic analysis of the subfamily to date.

Ancestral range estimation

We used the R package BioGeoBEARS v.1.1.2 (Matzke, 2018) to estimate ancestral ranges in Phanaeini. We relied on the BEAST MCC tree of the preferred analysis (see Results) without outgroups. Analyses were performed under the dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008) and a likelihood implementation of the DIVA analysis (Ronquist, 1997; i.e. DIVALIKE) model. We extrapolated the approximate geographical distribution of Phanaeini from relevant taxonomic literature (*op. cit.* above) and from study of locality data of specimens in the M. P. T. Gillett entomological collection and the Natural History Museums of Geneva, London and Paris. Owing in part to the convoluted and dynamic geological history of the New World continents (Mora *et al.*, 2009; Hoorn *et al.*, 2010; Hoorn & Wesselingh, 2011; Mastretta-Yanes *et al.*, 2015), ancestral range estimation of Neotropical taxa can prove recalcitrant to objective analysis. Furthermore, the ensuing delineation of vast landmasses into meaningful biogeographical areas is often highly subjective and open to ambiguous interpretation. For our analyses, we elected a simplified geographical division scheme, based in part on that used in several Neotropical studies summarized and adopted by Toussaint *et al.* (2019), which included the following eight coded regions: Nearctic (N), Mesoamerican lowlands (L), Mesoamerican highlands (H), Chocó (C), Andes (A), Amazonia (M), Cerrado (R) and Atlantic Forest (F) (Fig. 2A). In contrast to Toussaint *et al.* (2019), and because we analysed multiple taxa occurring in, or restricted to, the seasonally dry (mostly) open habitats of the Caatinga, Cerrado and Chaco, corresponding to the Chacoan subregion as defined in the Neotropical subdivisions of Morrone (2001), we have correspondingly included the 'Cerrado' area to encompass all these regions. The maximum number of areas per ancestral state was fixed to four, resulting in 163 possible ranges being explored.

We compared null models (M0), excluding a dispersal rate scaler and adjacency matrices with designed models, taking into account the geological evolution of the Nearctic and Neotropical regions through space and time. To do so, we relied upon five time slices set up as follows: TS1 (55–34 Mya), early stages of the Andean and Central American highland orogenies and emergence of the Pozo embayment, a large marine incursion limiting dispersal between the proto-Andes and eastern Amazonia (Hoorn *et al.*, 2010; Hoorn & Wesselingh, 2011); TS2 (34–23 Mya), disappearance of the Pozo embayment (Iturralde-Vinent & MacPhee, 1999; Iturralde-Vinent, 2006; Hoorn *et al.*, 2010; Hoorn & Wesselingh, 2011); TS3 (23–15 Mya), dynamic stages of the Andean and Central American highland orogenies, with the formation of the wetland Pebas system between the Atlantic and Pacific coasts (Wesselingh *et al.*, 2002; Wesselingh & Salo, 2006; Antonelli *et al.*, 2009; Hoorn *et al.*, 2010; Jaramillo *et al.*, 2017b; Hoorn & Wesselingh, 2011); TS4 (15–7 Mya), emergence of the Acre system, reducing dispersal between the Andean and Amazonian regions, and early stages of the Proto-Caribbean Seaway closure (i.e. formation of the Isthmus of Panama) (Bacon *et al.*, 2015; Montes *et al.*, 2015; Jaramillo *et al.*, 2017a; Jaramillo, 2018); and TS5 (7 Mya to present), most dynamic stages of the Andean orogeny, demise of the Acre system and final stages of the closure of the Proto-Caribbean Seaway (e.g. O'Dea *et al.*, 2016). We selected the dispersal rate scaler values according to the terrain and positions of water bodies throughout the timeframe of the evolution of the group (Supporting Information, Appendix S3).

Ancestral feeding biology and size estimation

We used the Bayesian binary Markov chain Monte Carlo (BBM) method as implemented in RASP v.4.2 (Yu *et al.*, 2020) to infer ancestral feeding biology and average size. Feeding biology was coded as one of the following four states: coprophagous (A), necrophagous (B), myrmecophilous (C) or unknown (D). The average size was based on maximum recorded species lengths reported in the taxonomic literature (*op. cit.* above), measured from the apex of the clypeus to the apex of the elytra, and arranged into the following five categories: very small (0–15 mm), small (15–20 mm), medium (20–25 mm), large (25–30 mm) and very large (≥ 30 mm) (Fig. 2B). The BEAST Markov chain Monte Carlo tree was used as an input for the BBM analysis. The BBM analyses were performed with estimated frequencies (F81+G) for five million generations, with ten chains and a chain temperature of 0.1.

Analyses of diversification dynamics

We used the program BAMM v.2.5.0 (Rabosky, 2014) to estimate putative diversification rates among and within clades of Phanaeini. The analyses were conducted with four reversible-jump Markov chain Monte Carlo runs for 1 million generations and sampled every 1000 generations. Optimal parameter priors were estimated beforehand in R (expectedNumberOfShifts = 1.0; lambdaInitPrior = 3.018; lambdaShiftPrior = 0.021; muInitPrior = 3.018). We used different values (0.1, 1, 2 and 5) for the parameter controlling the compound Poisson process that determines the prior probability of a rate shift along branches of the chronogram. Missing taxon sampling was taken into account by setting the global sampling fraction to 0.4, because assigning clade-specific sampling fractions would be too perilous considering the rampant paraphyly of genera in Phanaeini (see Results). We then analysed the BAMMoutput files using the R package BAMMtools v.2.1.6 (Rabosky *et al.*, 2014). The posterior distribution of the BAMM analysis was used to estimate the best shift configuration and the 95% credible set of distinct diversification models. Considering the ongoing debate regarding the reliability of results derived from this diversification rate analytical toolkit (Mitchell & Rabosky, 2017; Rabosky *et al.*, 2017; Meyer *et al.*, 2018; Meyer & Wiens, 2018; Rabosky, 2018, 2019), we remain cautious in our interpretation of these results and recommend readers be so likewise.

RESULTS

Phylogenetic relationships

Tribal-level relationships

The best-scoring tree from 300 independent tree searches conducted in IQ-TREE is presented in Figure 3 (see details in Supporting Information, Appendix S4). We recover Phanaeini as paraphyletic owing to the placement of *Gromphas* in a separate clade also containing the non-Phanaeini genera *Apotolamprus* d'Olsoufieff, 1947, *Ateuchus*, *Dichotomius* Hope, 1838 and *Nanos* Westwood, 1842 (Fig. 3).

We recover the Phanaeini* (Phanaeini excluding *Gromphas*, clade IV in Fig. 3) as sister to Eucraniini (clade III) with weak support (SH-aLRT = 62; UFBoot = 63). The monophyly of Phanaeini* is recovered with strong nodal support in the ML reconstruction (SH-aLRT = 100; UFBoot = 100) and in the BEAST analysis conducted on a smaller dataset [BEAST posterior probability (PP) = 1.0; Fig. 3; Supporting Information, Appendix S5]. Within Phanaeini, we recover *B. onitoides* + *Sulcophanaeus faunus* (Fabricius, 1775) (clade V) as sister to the remainder of the tribe in the ML reconstruction, with strong nodal support (SH-aLRT = 100; UFBoot = 100). In the BEAST reconstruction, *Diabroctis* is recovered as sister to the remainder of the tribe with weak support (PP = 0.62), although this discrepancy between ML and BI has no significance for the results of the biogeographical estimation (see Results).

Position of myrmecophilous taxa and relationships within Coprophanaeus

We recover *Megatharsis buckleyi* with low nodal support in a clade consisting of the three *Dendropaemon* species, i.e. all the analysed purported myrmecophilous species, and *C.* (*Metallophanaeus*) *pertyi* (SH-aLRT = 30; UFBoot = 16), wherein it is sister to *C. pertyi* with low nodal support (SH-aLRT = 26; UFBoot = 59; PP = 0.42). That clade is itself part of a clade containing the 12 included species of the nominate subgenus *Coprophanaeus* (*Coprophanaeus*) (SH-aLRT = 94; UFBoot = 65; PP = 0.98). That *Coprophanaeus* (*Coprophanaeus*) + *Dendropaemon* + *C. pertyi* clade is sister to a clade containing the remaining *Coprophanaeus* species included in the dataset, i.e. the four species of the subgenus *Coprophanaeus* (*Megaphanaeus*) [*C. bellicosus*, *C. bonariensis* (Gory, 1844), *C. ensifer* and *C. lancifer* (Linnaeus, 1767)] (SH-aLRT = 77; UFBoot = 70; PP = 0.74) and the two species of the *C.* (*Metallophanaeus*) *saphirinus* species group (*C. machadoi* and *C. saphirinus*). In summary, the myrmecophilous genus *Dendropaemon* and the genus *Megatharsis* are recovered within the *Coprophanaeus* (*Coprophanaeus*) clade (clade IX), which is sister to the two species of *Diabroctis* in the ML reconstruction (together forming clade VII; SH-aLRT = 35; UFBoot = 9), or as sister to *B. onitoides* + *S. faunus* in the BEAST inference (PP = 0.62). The subgenus *Coprophanaeus* (*Metallophanaeus*) is polyphyletic, with the *C. saphirinus* species group [recovered with strong support as monophyletic (SH-aLRT = 96; UFBoot = 97/ PP = 1.0)] being sister to the subgenus *Coprophanaeus* (*Megaphanaeus*) [also recovered with strong support as monophyletic (SH-aLRT = 100; UFBoot = 100; PP = 1.0)] in one clade, and the *C. thalassinus* species group [represented only by *C.* (*M.*) *pertyi*] nested within a clade comprising *Coprophanaeus* (*Coprophanaeus*) + *Dendropaemon* + *Megatharsis*.

Within the genus *Coprophanaeus s.l.*, all species groups available for monophyly testing were recovered as monophyletic, as follows: within the nominate *Coprophanaeus* (*Coprophanaeus*), the *Coprophanaeus jasius* (Olivier, 1789) species group (two spp.) (SH-aLRT = 80/UFBoot = 64; PP = 0.44), the *Coprophanaeus dardanus* (MacLeay, 1819) species group (four spp.) (SH-aLRT = 88; UFBoot = 93; PP = 1.0) and the *Coprophanaeus pluto* (Harold, 1863) species group (six spp.) (SH-aLRT = 84; UFBoot = 91; PP = 0.89); within *Coprophanaeus* (*Megaphanaeus*), the *lancifer* species group (three spp.) (SH-aLRT = 100; UFBoot = 100; PP = 1.0); and within *Coprophanaeus* (*Metallophanaeus*), the *saphirinus* species group (two spp.) (SH-aLRT = 96; UFBoot = 97; PP = 1.0).

Relationships among Phanaeus and related genera

We recover the *Coprophanaeus* clade (also containing the myrmecophilous taxa) as sister to *Diabroctis* in ML or sister to *Bolbites* + *S. faunus* in BEAST (as outlined above), and these two alternative clades (i.e. ML or BEAST) are each sister to *Phanaeus* + *Oxysternon* + *Sulcophanaeus* (minus *S. faunus*) (SH-aLRT = 92; UFBoot = 44; PP = 0.62). *Oxysternon* is split across two polyphyletic clades, in one of which, the two species *Oxysternon* (*Mioxysternon*) *spiniferum* Castelnau, 1840 and *Oxysternon* (*Oxysternon*) *silenus* Castelnau, 1840 are sister to three *Sulcophanaeus* species belonging to the *Sulcophanaeus auricollis* (Harold, 1880) species group [*S. auricollis*, *Sulcophanaeus noctis* (Bates, 1887) and *Sulcophanaeus velutinus* (Murray, 1856)] (clade X, SH-aLRT = 89; UFBoot = 37; PP = 0.74), and in the other, the remaining four analysed *Oxysternon* species, all in the nominate subgenus *Oxysternon* (*Oxysternon*), are recovered nested within *Phanaeus* (clade XI), in a clade containing eight South American species of the subgenus *Phanaeus* (*Notiophanaeus*) [specifically members of the *Phanaeus bispinus* Bates, 1868, *Phanaeus palaeno* Blanchard, 1846 and *Phanaeus splendidulus* (Fabricius, 1781) species groups] (SH-aLRT = 91; UFBoot = 71; PP = 1.0). Within this clade, the cerrado habitat specialist *Phanaeus* (*Notiophanaeus*) *palaeno* species group (*Phanaeus kirbyi* Vigors, 1825 and *P. palaeno*) is recovered as monophyletic (SH-aLRT = 100; UFBoot = 100; PP = 1.0).

That *Oxysternon* + *Phanaeus* (*Notiophanaeus*) (in part) clade is sister to all other analysed *Phanaeus*, i.e. all species of the subgenus *Phanaeus* (*Phanaeus*), plus the predominantly South American *Phanaeus chalcomelas* (Perty, 1830) species group and the predominantly Central American *Phanaeus endymion* Harold, 1863 species group, both currently assigned to the subgenus *Phanaeus* (*Notiophanaeus*) (SH-aLRT = 78; UFBoot = 58; PP = 0.86). Within this last mentioned *Phanaeus* clade, the following *Phanaeus* (*Phanaeus*) species groups are recovered as monophyletic: the *Phanaeus vindex* MacLeay, 1819 species group (three spp.) (SH-aLRT = 90; UFBoot = 97; PP = 0.99); *Phanaeus tridens* Castelnau, 1840 species group (three spp.) (SH-aLRT = 100; UFBoot = 100; PP = 0.96); the *Phanaeus amethystinus* Harold, 1863 species group (two spp.) (SH-aLRT = 100; UFBoot = 100; PP = 1.0); and the *Phanaeus hermes* Harold, 1868 species group (two spp.) (SH-aLRT = 93; UFBoot = 99; PP = 0.80). Additionally, in the same clade, the *P. endymion* species group (three spp.), currently assigned to *Phanaeus* (*Notiophanaeus*), was recovered as monophyletic (SH-aLRT = 92; UFBoot = 99; PP = 1.0). Notably, the *Phanaeus mexicanus* Harold, 1863 species group of *Phanaeus* (*Phanaeus*), represented by five species (*Phanaeus demon* Castelnau, 1840, *Phanaeus wagneri* Harold, 1863, *Phanaeus amithaon* Harold, 1875, *Phanaeus lunaris* Taschenberg, 1870 and *Phanaeus yecoraensis* Edmonds, 2004), is paraphyletic, although a constituent species-pair, *P. amithaon*/*P. wagneri*, was recovered as monophyletic (SH-aLRT = 98; UFBoot = 99; PP = 1.0). Likewise, the *Phanaeus beltianus* Bates, 1887 species group, with four analysed species (*P. beltianus*, *Phanaeus changdiazi* Kohlmann & Solís, 2001, *Phanaeus howdeni* Arnaud, 1984 and *Phanaeus sallei* Harold, 1863) was also recovered as paraphyletic.

Macroevolution of Phanaeini*

The results of the different BEAST analyses are presented in Table 1. The analysis based on two clocks and a Yule speciation model received the best marginal likelihood estimate as computed by both path-likelihood and stepping-stone sampling (Table 1). The divergence time estimates and phylogenetic relationships are largely consistent across analyses. Hence, we present the results of the preferred analysis, from which a summary chronogram is presented in Figure 4 (see details in Supporting Information, Appendix S5). The results of the BioGeoBEARS analyses are presented in Table 2. The designed models (M1), taking into account the geological history of the Nearctic and Neotropical regions, were significantly supported in comparison to the null models (M0) in both DEC and DIVALIKE models. However, all analyses across all models recovered an origin of Phanaeini* in a joint area comprising the Amazonian basin and the Cerrado region in the early Eocene, ~55 Mya. Given that the M1 DIVALIKE model received the best support (LnL = –167.62; Table 2), we present the results of this analysis, but detailed results of the other models are available in the Supporting Information (Appendices S6 and S7). A subsequent vicariant event led to the formation of a Cerrado lineage, later resulting in the *Diabroctis* clade (Fig. 4), and an Amazonian lineage comprising the remainder of the Phanaeini. The Atlantic Forest biome was colonized by *Coprophanaeus*

Table 1. Results of the Bayesian estimation of divergence times (in millions of years ago) performed in BEAST

Analysis	Clock model	Tree model	PS MLE	SS MLE	BEAST likelihood	Phanaeini* TMRCA
A1	1 ULRC	Yule	−23 550.946	−23 550.570	−23 049.932	50.778 (36.800–65.555)
A2	1 ULRC	Birth–death	−23 552.233	−23 552.204	−23 049.596	50.914 (37.220–66.082)
A3	2 ULRC	Yule	−23 465.910	−23 466.213	−22 904.217	54.109 (42.421–69.604)
A4	2 ULRC	Birth–death	−23 467.181	−23 467.470	−22 904.896	53.847 (41.908–68.917)
A5	6 ULRC	Yule	−23 490.049	−23 490.188	−22 871.274	52.524 (42.383–66.863)
A6	6 ULRC	Birth–death	−23 490.870	−23 490.332	−22 870.632	52.609 (41.400–65.849)

The median age and 95% credibility interval is given for the crown of Phanaeini*.
Abbreviations: MLE, marginal likelihood estimate; PS, path sampling; SS, stepping-stone sampling; TMRCA, the most recent common ancestor; ULRC, uncorrelated lognormal relaxed clock.

through range expansion as early as the late Eocene, ~35–40 Mya, with a subsequent vicariant event leading to one clade inhabiting the Atlantic Forest and one clade occupying the Amazon basin. The latter clade then colonized the Mesoamerican lowlands through range expansion in the Oligocene by crossing the Proto-Caribbean Seaway. A subsequent vicariant event led to a lineage inhabiting the Mesoamerican lowlands and another the Amazonian region. The former then colonized the Mesoamerican highlands during the Miocene.

The Andes were colonized from Amazonia in the early Oligocene by members of the clade comprising *Sulcophanaeus* and *Oxysternon* (Fig. 4). We infer a second crossing of the Proto-Caribbean Seaway in this clade via range expansion.

In the genus *Phanaeus*, we estimate that colonization of the Atlantic Forest occurred during the Oligocene and that of the Cerrado during the Miocene, both through range expansion from the Amazonian region. We finally infer a dispersal event from the Amazonian region towards the Chocó region during the Oligocene, followed by range expansion towards the Mesoamerican lowlands in the Oligocene, resulting from a third crossing of the Proto-Caribbean Seaway. The Nearctic region and the Mesoamerican highlands were later both colonized during the Miocene (Fig. 4).

The results of the BBM analyses focusing on diet evolution are summarized in Figure 4. We estimate that coprophagy was the ancestral feeding biology when Phanaeini* originated and that a unique shift towards necrophagy occurred in the late Eocene at the crown of the clade comprising *Coprophanaeus*, *Dendropaemon* and *Megatharsis* (Fig. 4). After this shift, we estimate two secondary transitions from necrophagy towards myrmecophily in *Dendropaemon*.

The results of the different BAMM analyses are presented in Table 3. Our analyses reveal no supported shift in diversification dynamics across the phylogeny and throughout the evolution of Phanaeini*, with a declining speciation rate through time.

DISCUSSION

TRIBAL-LEVEL RELATIONSHIPS

The placement of *Gromphas* outside of Phanaeini with moderate support (Fig. 3) is not a new result, because this has already been suggested by the phylogenetic reconstructions of Monaghan *et al.* (2007) and Gunter *et al.* (2016) using similar data. Although molecular sequence data for three contentious phanaeine genera (*Gromphas*, *Oruscatus* and *Bolbites*) have never been analysed together, no molecular reconstruction that has included *Gromphas* has ever recovered the Phanaeini as monophyletic. However, this is

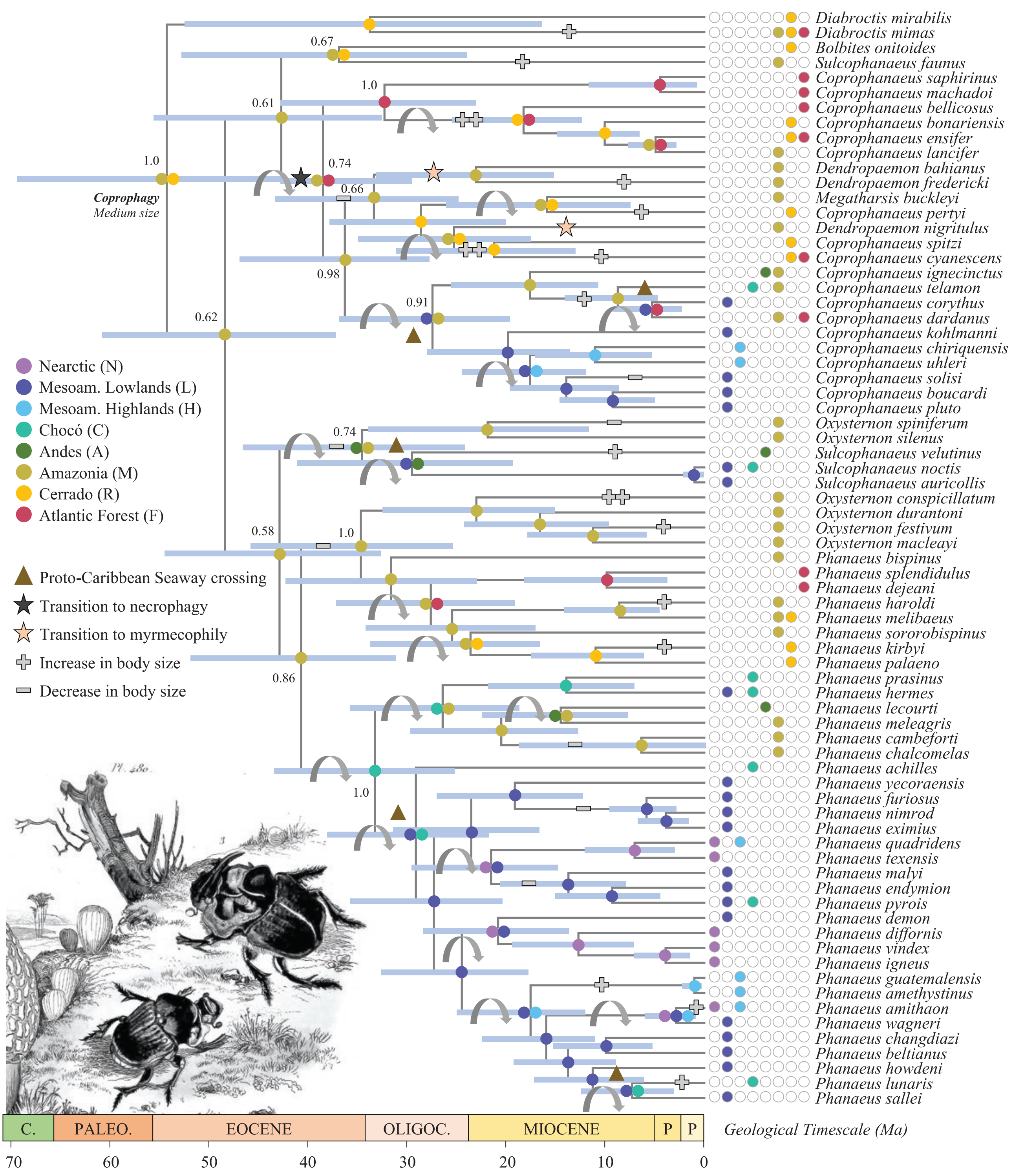

Figure 4. Divergence times and historical biogeography of Phanaeini scarab beetles in the New World. Maximum clade credibility chronogram derived from the best BEAST analysis as selected based on comparison of marginal likelihood estimates (two uncorrelated lognormal relaxed clocks and a Yule tree model). Grey arrows represent range expansion/dispersal events across the phylogeny. Inset is an engraving from '*Dictionnaire pittoresque d'histoire naturelle et des phénomènes de la nature*', edited by Félix-Édouard Guérin-Méneville (1838), depicting two 'Phanées': *Coprophanaeus bonariensis* (Gory, 1844) and *Diabroctis mimas* (Linnaeus, 1758) (credit: Biodiversity Heritage Library).

Table 2. Results of the ancestral range estimation performed in BioGeoBEARS

Model	LnL	nparams	*d*	*e*	Origin Phanaeini*	AIC
M0 DEC	−185.10	2	0.0028	0.0041	MR	339.24
M0 DIVALIKE	−182.73	2	0.0032	0	MR	374.20
M1 DEC	−171.18	2	0.0065	0.0037	MR	346.36
M1 DIVALIKE	−167.62	2	0.0074	0	MR	369.46

Abbreviations: AIC, Akaike information criterion; *d*, dispersal rate; *e*, extinction rate; LnL, log-likelihood calculated in BioGeoBEARS; M, Amazonia; nparams, number of parameters in the analysis; R, Cerrado.

Table 3. Results of the diversification dynamics analysis performed in BAMM

Prior shift no.	ESS shift no.	ESS LnL	PD (zero shift)	PD (one shift)	PD (two shifts)
0.1	901	773	0.99	0.01	0
1	818	649	0.92	0.061	0.013
2	663	797	0.90	0.093	0.009
5	580	496	0.85	0.12	0.021

Abbreviations: ESS, effective sample size; LnL, log-likelihood; PD, Bayesian posterior distribution for a particular shift configuration.

in contrast to morphological analyses, which have inferred *Gromphas* as belonging to a monophyletic Phanaeini (Philips *et al.*, 2004; Cupello & Vaz-de-Mello, 2016). That *Gromphas* is peculiar from other Phanaeini is amply demonstrated by the fact that recently it was recognized (together with *Oruscatus*, not studied in our dataset) as belonging in a separate subtribe, the Gromphadina (Cupello & Vaz-de-Mello, 2016). However, despite the fact that in that study a morphological phylogeny of all species of *Gromphas* confirmed its monophyly and established an internal topology, no meaningful insights could be made into its relationship to other genera because only two outgroup taxa were analysed (Cupello & Vaz-de-Mello, 2016). Our analysis of an expanded taxon sample is in agreement with previous molecular results: *Gromphas* does not belong in Phanaeini. Unlike Edmonds (1972), who excluded *Gromphas* from the phanaeines ‘confidently, but at the same time, reluctantly’, with the additional data we are now confident of its exclusion, based upon our molecular data. However, like him, we are reluctant to offer an alternative tribal placement for the genus without further investigation.

Our recovery of Phanaeini* as sister to Eucraniini with weak support (SH-aLRT = 62; UFBoot = 63) is similar to earlier molecular and morphological phylogenies (Philips *et al.*, 2004; Ahrens *et al.*, 2014; Gunter *et al.*, 2016; Tarasov & Dimitrov, 2016).

Within Phanaeini, the recovery of *B. onitoides* + *S. faunus* (clade V in Fig. 3) as sister to the remainder of the tribe in the ML reconstruction with strong nodal support (SH-aLRT = 100; UFBoot = 100), or of *Diabroctis* as sister to the remainder of the tribe in the BEAST inference with weak support (PP = 0.62), is similar to the findings of Philips *et al.* (2004), who inferred these lineages as basal to the remainder of the tribe in some of their cladistic analyses of morphological characters.

PHYLOGENY OF *COPROPHANAEUS* AND POLYPHYLY OF *METALLOPHANAEUS*

After a detailed morphological assessment of many genera of Phanaeini, Edmonds (1972) concluded that the nominate subgenus of *Coprophanaeus*, sharing many synapomorphies with members of the genus *Dendropaemon* [especially the subgenus *Dendropaemon* (*Coprophanaeoides*) Edmonds, 1972], is more closely related to that genus than it is to either the subgenera *Coprophanaeus* (*Megaphanaeus*) or *Coprophanaeus* (*Metallophanaeus*), suggesting that *Coprophanaeus s.l.* is paraphyletic. Our study supports this assertion, because we recover *Coprophanaeus s.l.* divided into two lineages: one containing the *Coprophanaeus* (*Megaphanaeus*) + *C. saphirinus* group of *Coprophanaeus* (*Metallophanaeus*), and a second containing the *Coprophanaeus* (*Coprophanaeus*) + *C. thalassinus* group of *Coprophanaeus* (*Metallophanaeus*) + *Dendropaemon* + *Megatharsis* (Fig. 3).

When d’Olsoufieff, 1924) erected the subgenus *Coprophanaeus* (*Metallophanaeus*), he distinguished its members from those of the nominate subgenus primarily by the long, upright and acuminate cephalic horn and by the two dentiform pronotal protuberances of the males. He assigned only two species to the new subgenus [*C. saphirinus* and *Coprophanaeus horus* (Waterhouse, 1891)], each clearly possessing the diagnostic characteristics. Subsequently, Edmonds (1972) incorporated two additional species into *Coprophanaeus* (*Metallophanaeus*) (*C. pertyi* and *C. thalassinus*; neither of which possesses the morphological characteristics that d'Olsoufieff had used to define the subgenus), grouping these four species together primarily based upon their hindwings not being notched basally, whilst simultaneously recognizing that the latter pair of species were distinct from the original pair of included species. Edmonds evidently deemed this distinction to be significant, although he also could not then justify the erection of a separate subgenus for *C. pertyi* and *C. thalassinus* (Edmonds, 1972). The current classification of *Coprophanaeus* (*Metallophanaeus*) (Arnaud, 2002; Edmonds & Zidek, 2010; Cupello & Vaz-de-Mello, 2014b) divides the subgenus into two species groups, each containing four described species, namely, the *C. saphirinus* group, containing four species that match morphologically d'Olsoufieff's (1924) subgeneric definition closely [*C. saphirinus*, *C. horus*, *Coprophanaeus punctatus* (d'Olsoufieff, 1924) and *Coprophanaeus machadoi* (Pereira & d'Andretta, 1955)], and the *C. thalassinus* group, whose members lack both dentiform pronotal projections and a long, upright cephalic horn, consisting of *C. thalassinus*, *Coprophanaeus pessoai* (Pereira, 1949), *C. pertyi* and *Coprophanaeus vazdemeloi* Arnaud, 2002). In the last major review of the genus *Coprophanaeus,* Edmonds & Zidek (2010) highlighted both the morphological affinity that the *C. saphirinus* group has with the subgenus *Coprophanaeus* (*Megaphanaeus*) and the affinity that the *C. thalassinus* group has with the *C. jasius* species group of the nominate subgenus, even going so far as to suggest that a 'cogent argument can be made to isolate the two species groups of *Coprophanaeus* (*Metallophanaeus*) into separate subgenera', whilst also recommending that 'any decision otherwise should await a more formal phylogenetic analysis of the entire *Coprophanaeus* lineage, including *Dendropaemon*'. In a recent molecular phylogenetic analysis focusing on the subgenus *Coprophanaeus* (*Megaphanaeus*), Maldaner *et al.* (2020) corroborated the idea of a close relationship between the *C. saphirinus* group and *Coprophanaeus* (*Megaphanaeus*) as proposed by Edmonds & Zidek (2010). They recovered these taxa as sister groups with moderate to high statistical support, whilst also suggesting that future studies should especially include members of the *thalassinus* group of *Coprophanaeus* (*Metallophanaeus*) and *Dendropaemon* in order to investigate relationships in these beetles further. Consequently, the cohesion of *Coprophanaeus* (*Metallophanaeus*) has been in doubt for some time.

Our molecular analyses, incorporating sequence data from all three subgenera of *Coprophanaeus* and, for the first time, both species groups of *Coprophanaeus* (*Metallophanaeus*), in addition to *Dendropaemon* and *Megatharsis*, do not support the monophyly of *Coprophanaeus* (*Metallophanaeus*). We infer the *C. thalassinus* group within a clade containing *Dendropaemon* and *Megathasris*, which itself forms part of the *Coprophanaeus* (*Coprophanaeus*) clade, being sister to the clade containing all species groups except the *C. jasius* group. The *C. saphirinus* group however, is recovered in a clade containing members of the subgenus *Coprophanaeus* (*Megaphanaeus*) (Fig. 3). Furthermore, both of these observed relationships are consistent with those suspected by Edmonds & Zidek (2010). Although we contemplated formally describing a new subgenus to accommodate the four species in the *thalassinus* species group, a comprehensive morphological reappraisal is beyond the scope of this work. Moreover, we believe that it is prudent to await the time when results of a more comprehensive phylogenetic analysis, preferably one containing most, if not all, species of *Coprophanaeus* (*Metallophanaeus*), are available.

PHYLOGENETIC PLACEMENT OF *MEGATHARSIS* AND *DENDROPAEMON* (*EURYPODEA*) *FREDERICKI*

The monobasic genus *Megatharsis*, containing only the very rarely sampled species *Megatharsis buckleyi* (Larsen *et al.*, 2006; Gillett *et al.*, 2009), possesses a unique combination of morphological characters, including the characteristic shape of its meso- and meta-tarsi. Although certain characters were recognized as resembling those of *Coprophanaeus*, Edmonds (1972) concluded that *Megatharsis*, together with the monobasic genera *Homalotarsus* and *Tetramereia* [now the subgenus *Dendropaemon* (*Eurypodea*)], are relict species of doubtful affinity to the *Coprophanaeus*–*Dendropaemon* lineage. However, the subsequent morphological phylogenetic analyses undertaken by Philips *et al.* (2004) did not support this assertion, because they inferred *Megatharsis* either nested within a clade containing *Coprophanaeus* and *Dendropaemon* [including *Dendropaemon* (*Eurypodea*)] or as the basal member in such a clade. Our own molecular results place *Megatharsis* within the *Coprophanaeus*–*Dendropaemon* lineage and are therefore congruent with the previous morphological analyses of Philips *et al.* (2004), and consequently, the agreement between these two independent datasets is compelling evidence for such a relationship.

The convoluted taxonomic history of the species presently known as *Dendropaemon* (*Eurypodea*) *fredericki* was summarized in the recent revision of the genus *Dendropaemon* (Génier & Arnaud, 2016).

These authors, implementing a new subgeneric structure for the genus based upon objective morphological phylogenetic analysis, concluded that the species formerly known as *Tetramereia convexa* is nested within *Dendropaemon* as the subgenus *Eurypodea*. Our results, incorporating sequence data for *Dendropaemon* (*Eurypodea*) for the first time and recovering it with moderate support (SH-aLRT = 95; UFBoot = 76) as sister to *Dendropaemon* (*Glaphyropaemon*) *bahianus* (GenBank sequences for this taxon derive from an Ecuadorian specimen that is most likely to be *Dendropaemon angustipennis* Harold, 1869), in a clade also containing *Dendropaemon* (*Nigropaemon*) *nigritulus* Génier & Arnaud, 2016 and *Megatharsis* [in addition to *C.* (*Metallophanaeus*) *pertyi*], although not conclusively in agreement, suggest that inclusion of *D. fredericki* in *Dendropaemon* is probably justified. Only further molecular analysis including a greater representation of the now 41 recognized species (in 12 subgenera) of *Dendropaemon* will test this fully. However, this is unlikely to happen soon, given the general rarity of these beetles.

RELATIONSHIPS AMONG *PHANAEUS* AND RELATED GENERA, AND PARAPHYLY OF *PHANAEUS* (*NOTIOPHANAEUS*)

Our analysis of an expanded taxon sample in comparison to the study by Price (2009) is largely congruent with their results; but whereas Price retrieved several *Coprophanaeus* species nested within *Phanaeus* + *Oxysternon* + *Sulcophanaeus*, we recover *Coprophanaeus* in a clade that is sister to *Diabroctis* in ML and sister to *Bolbites* + *S. faunus* in BEAST, and these two alternative clades are sister to *Phanaeus* + *Oxysternon* + *Sulcophanaeus* (minus *S. faunus*) (Figs 3, 4).

Our analyses infer the subgenus *Phanaeus* (*Notiophanaeus*) to be paraphyletic, with the analysed species of that subgenus being recovered in three disparate clades across the large *Phanaeus* + *Oxysternon* + *Sulcophanaeus* (except *S.faunus*) clade (Fig. 3). This result is, to a great extent, congruent with that obtained by Price (2009), and we note that all *Phanaeus* (*Notiophanaeus*) species whose males bear spiniform processes on the pronotum, together with the two South American Cerrado specialists, *P. kirbyi* and *P. palaeno*, are recovered in a clade (together with four Amazonian *Oxysternon* species) that is sister to all other analysed *Phanaeus*. This might prove, upon further analysis, to represent a natural taxon. The other *Phanaeus* (*Notiophanaeus*) are the species in the *endymion* and *chalcomelas* groups, whose males bear a triangular pronotum that is similar to that borne by many species belonging to the nominate subgenus *Phanaeus*. We believe that there is now sufficient evidence to cast doubt on the reliability and validity of the primary morphological character that has hitherto been used to diagnose the subgenus *Phanaeus* (*Notiophanaeus*); namely, the relative smoothness of the surface sculpture of the anterolateral portion of the pronotum. A reappraisal of morphological characters should now be undertaken in light of the molecular evidence presented here and in previous studies (e.g. Price, 2009).

Based primarily upon knowledge of past vegetation structure in Mexico, Kohlmann *et al.* (2018) suggested that the *P. endymion* species group of *Phanaeus* (*Notiophanaeus*) spread into Central America from South America during the Miocene, and not during the Pleistocene as suggested by Edmonds (1994). Moctezuma & Halffter (2017) also suggest the Plio-Pleistocene as a likely period when the *P. endymion* species arrived in Mexico. Our divergence time analyses and ancestral range estimation support the rise and initial diversification of the *P. endymion* group as taking place during the Miocene, as postulated by Kohlmann *et al.* (2018), although more recent diversification, giving rise to the full extant diversity of the group, could have occurred more recently. The first arrival of *Phanaeus* into Mesoamerica, however, occurred much earlier, probably during the Oligocene (Fig. 4).

Unsurprisingly, like Price (2009), we recover a polyphyletic genus *Oxysternon* in two clades, one of which is nested within *Phanaeus s.l*. The only species additional to Price's dataset that we analysed, *Oxysternon macleayi* (Nevinson, 1892), was recovered within a clade containing three other Amazonian *Oxysternon* species with close relationships morphologically, whereas two morphologically divergent species, including one belonging to the subgenus *Oxysternon* (*Mioxysternon*) (*Oxysternon spiniferum* Laporte, 1840) were recovered in another clade (together with three *S. auricollis* species group species) that is sister to all *Phanaeus* plus the four aforementioned *Oxysternon* nested within it (Fig. 3).

In one of the morphologically derived consensus trees presented by Philips *et al.* (2004), *S. faunus* was recovered in a basal clade together with the distinctive Jamaican *Sulcophanaeus carnifex* (Linnaeus, 1758) (the only species of Phanaeini occurring in the Antilles). Each of those species is classified at present in a separate species group (two of the five species groups in the genus). *Sulcophanaeus*, as has previously been suggested (e.g. Edmonds, 2000; Philips *et al.*, 2004), is a paraphyletic assemblage of multiple species groups, some of which (almost certainly at least the *S. faunus* species group) might warrant generic or subgeneric recognition once they have all been analysed together in the future.

HISTORICAL BIOGEOGRAPHY, DIVERSIFICATION AND EVOLUTION OF NON-COPROPHAGOUS FEEDING BIOLOGY

Our BEAST and BioGeoBEARS analyses unequivocally recover an origin of Phanaeini* in the Eocene, ~55 Mya, probably in eastern South America (Fig. 4). The fact that null models and designed models recover sensibly similar patterns of ancestral range evolution seems to indicate that the major Cenozoic geological events within the Neotropics had little impact on the evolutionary trajectory of these beetles. For instance, Andean orogeny occurred throughout the evolution of Phanaeini*, yet these beetles did not colonize the Andean mountainous regions extensively, nor do they seem to have suffered from reduced trans-Andean range expansions. In the same vein, Phanaeini* ancestors repeatedly reached Central America long before the formation of the Isthmus of Panama (Bacon *et al.*, 2015; Montes *et al.*, 2015; O'Dea *et al.*, 2016; Jaramillo, 2018), possibly when a Proto-Panamanian archipelago allowed short oversea dispersal between South American and Central America (Pindell *et al.,* 1988, 2005; Iturralde-Vinent, 2006). Such a biogeographical pattern was recently suggested for Anaeini leafwing butterflies (Toussaint *et al.*, 2019). Additionally, fossil dung beetle brood balls dating from the Eocene to Oligocene have been recovered in the Nearctic region, supporting the pre-Pliocene presence of dung beetles of the subfamily Scarabaeinae in North America (Krell, 2000). Overall, Phanaeini* beetles had a dynamic biogeographical history, mostly suggesting that Amazonia served the role of both a cradle and a museum of diversity, as has recently been suggested for other taxa (Antonelli *et al.*, 2018). Interestingly, we estimate very few reverse colonization events, possibly indicating that these beetles occupy highly competitive ecological niches. This intensive competition, especially for resources linked to their diet, might have been the major trigger explaining the shift from coprophagy to necrophagy in *Coprophanaeus*, because both biogeography and lineage-specific diversification dynamics appear to be unlinked to dietary shifts.

Competing hypotheses for the evolution of myrmecophilous/inquilinous behaviour in Phanaeini have been put forward based upon morphological phylogenetic analyses. Philips *et al.* (2004) concluded that 'myrmecophily is also derived and most likely evolved only once', whereas Génier & Arnaud (2016) concluded that, although like *Dendropaemon*, the morphology of *Megatharsis* and *Homalotarsus* suggests that they are inquilines, 'they belong to a different clade and this behaviour would have evolved separately'. Consideration of our ML reconstruction instead of the BEAST one would be likely to result in a unique shift towards myrmecophily; therefore, additional data will be needed to gain a better understanding of the number of shifts in this clade. Given that *C. pertyi* is necrophagous, and based on the overall estimation of feeding biology in this clade, it is not unlikely that *Megatharsis* is a necrophagous lineage, but here too, additional data are needed. The shift in feeding biology seems to be unrelated to the biogeographical history of the tribe, because the *Coprophanaeus* + *Dendropaemon* + *Megatharsis* clade is of Amazonian origin, whereas other clades in Phanaeini originating in the same region contemporaneously remained largely coprophagous. Size, in contrast, might be correlated with shifts in feeding biology, at least in relationship to myrmecophily, because species shifting towards this lifestyle also simultaneously shift from a medium size to a smaller size in concert (Fig. 4).

The hypothesis that a switch from coprophagy to necrophagy occurred owing to the mass extinction of the Pleistocene mammalian megafauna in South America (e.g. Halffter & Halffter, 2009) is inconsistent with our ancestral feeding biology estimation. According to our analysis, within the Phanaeini, a unique evolutionary shift to necrophagy occurred during the late Eocene by the *Coprophanaeus* + *Dendropaemon* + *Megatharsis* clade (Fig. 4). Consequently, we infer that Phanaeini taxa were feeding on carrion long before the mass extinction of the South American mammalian megafauna.

We have corroborated prior morphological inference suggesting that the enigmatic genus *Megatharsis* is closely allied to the genus *Dendropaemon*, of suspected myrmecophilous habits. Furthermore, we concur with the notion that myrmecophily is a derived behaviour, because the myrmecophilous Phanaeini appear in an apical position within the necrophagous *Coprophanaeus* clade, and we advance that opinion by suggesting that this condition has probably arisen once from predominantly necrophagous ancestral species, ~35 Mya during the Eocene–Oligocene boundary.

We hope that the systematic implications outlined above will be contemplated seriously through continued analysis of ever-augmentative datasets, such that these alluring and handsome beetles will long retain their deserved standing amongst the best-known of scarab beetles.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Concatenated molecular dataset.
Appendix S2. ModelFinder optimal partitioning scheme.
Appendix S3. BioGeoBEARS M1 model stratification details.
Appendix S4. IQ-TREE best scoring tree.
Appendix S5. BEAST chronogram 2 clocks Yule tree model.
Appendix S6. BioGeoBEARS M0 model results.
Appendix S7. BioGeoBEARS M1 model results.